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THE DIRECTIVE INFLUENCE OF LIGHT ON THE GROWTH OF FOREST PLANTS.

BY JOHN W. HARSHBERGER, PH.D.

It is a well-known fact that light exercises a directive influence upon plants. This directive influence is called heliotropism, or phototropism. When a plant is grown in the window of a room, so that it is unequally illuminated, that is, more powerfully through the window, its leaves and even its stem are turned toward the incident rays of light. This is known as positive heliotropism. If the common English ivy, *Hedera helix*, be grown in pots by a north window, so as to emphasize better the difference in light intensities, in about four weeks it will be apparent that the growing sprouts are bending toward the inner part of the room, away from the stronger light. This reaction is negative heliotropism.

The growth of forest plants is largely a question of light relationship. Foresters recognize this fact and group trees into those intolerant of the shade and those that are tolerant. The herbaceous plants, likewise, are influenced by the light which filters through the crown of leaves above. The herbaceous spring flora of the forest requires more light than the relatively few plants which flower in the autumn require, when the trees are covered with foliage. These facts, although they can be proved experimentally, are not always demonstrable to the uninitiated. One of the best illustrations that the writer has seen is the directive influence of light upon the leaves, or fronds, of the hay-scented fern, *Dicksonia pilosiuscula* (= *Dennstaedtia punctilobula*), which is widely distributed on open hillsides from New Brunswick and Ontario to Indiana and Minnesota, south to Alabama and Tennessee, ascending to 1680 m. in Virginia. The stipes of this fern are pale green and chaffless, covered with fine hairs, and the leaves (10 dm. long, 12-20 cm. wide) are ovate-lanceolate, acute or acuminate, frequently long attenuate, usually tri-pinnatifid, thin and delicate in the woods, tougher, more inrolled and more erect in the sun; rachis and under surface of blades glandular pubescent. The observations which the writer wishes to record on the directive influence of light upon the position of the fronds were made at Pocono Pines, Monroe County, Pennsylvania, where this fern is one of the most abundant species. As the photograph will show (Pl. XXIV), the upper surfaces

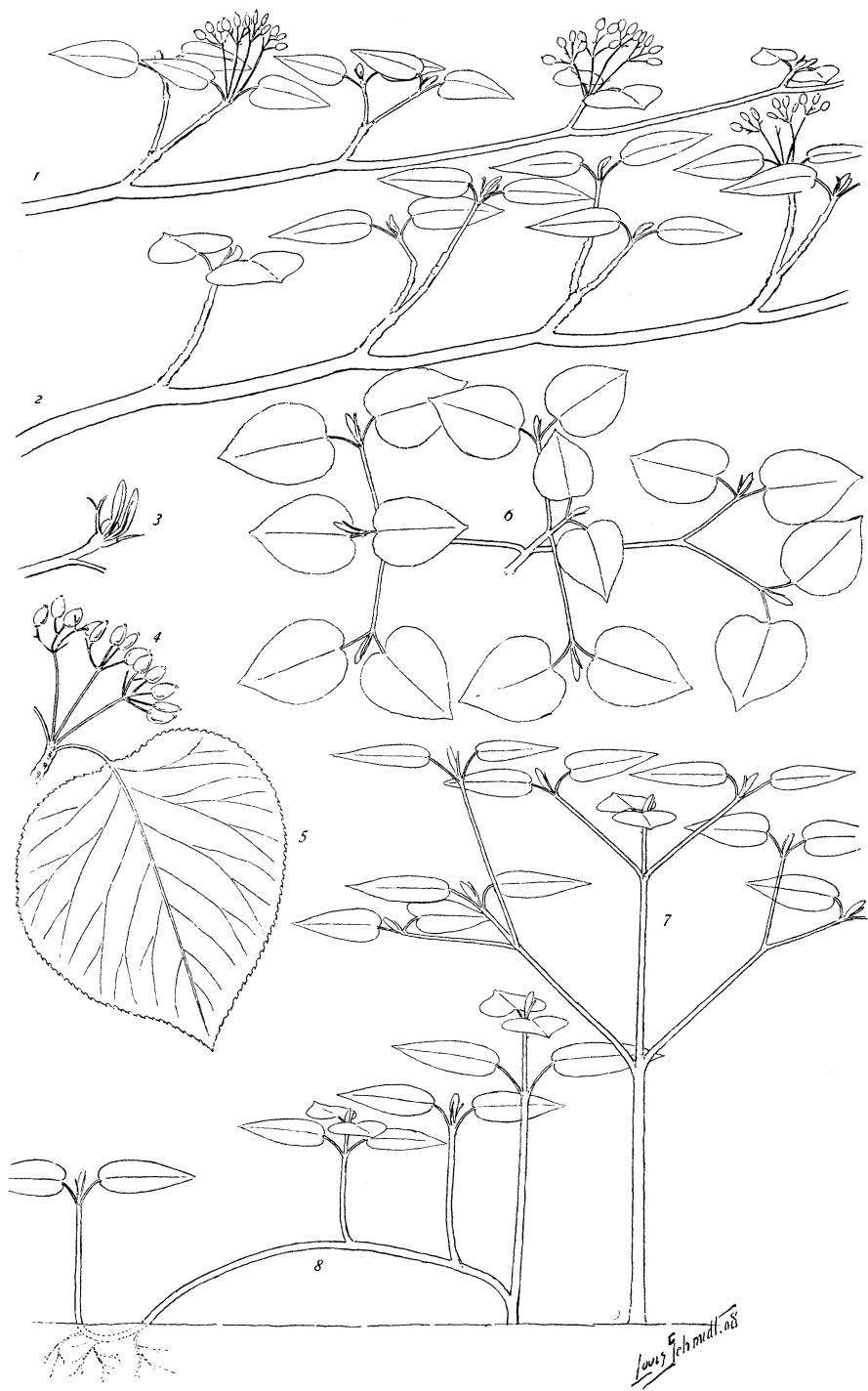
of the leaves are turned toward the light, if the illumination is one-sided. If the illumination is from all sides of the fern clump, then there is no particular direction in which the leaf-blades face. The one-sided illumination is obtained when the ferns grow along the edge of the woods, composed in the Pocono region of white pines, white birches, black spruces, beeches and maples, which on account of their dense crown cut off much of the light from behind and above, so that such woods can be called appropriately dark woods. The photograph shows how all the leaves of a single patch are turned outward toward the open field adjoining the woods, in obedience to the directive influence of the light, so that the leaves stand, row after row, all facing in one direction.

The second and more striking example of the directive influence of light is illustrated by the hobble-hush, *Viburnum lantanoides* (= *V. alniifolium*), a shrub which ranges from New Brunswick to North Carolina, western New York and Michigan, but which does not occur in the woods near the City of Philadelphia. In the dark pine woods on the Pocono plateau this shrub is extremely abundant, and where the woods are the densest, not only are all of the branches and the leaves directed by the incident rays of light, but they show permanent structural changes which are induced by the directive light influence. It is known that light has a most notable influence in the determination of the external form of a large number of plants. The development of certain tissues or organs on one side of the axis of a shoot, and their suppression on other parts of the plant body, may be regulated experimentally by means of the character of the illumination. This development of tissues on one side of the axis is illustrated finely in the branches of adult forest-grown specimens of the hobble-bush. If we examine young shrubs of this plant, illustrated in Pl. XXV, fig. 7, we see that the branching system follows the method of a dichasium. The leaves in such young bushes stand perfectly horizontal, so as to receive the incident rays of light on the upper surface of the blade, and so as to present their profile to the observer standing in front of the plant. As fig. 6 shows, they arrange themselves, when viewed from above, in the pattern of a leaf mosaic, so that none of the leaves overshadow the others. Such plants merely show the directive influence of the light on the leaves, without showing any characteristic growth differences. The same influence of light is manifested in the stoloniferous branches which strike root, and which give the common names hobble-bush or trip-toe to the plant (fig. 8). These plagiotropous shoots are only formed in the shade. The diminished light

can be better used by such branches, to which the moist soil offers at the same time an opportunity to root. Such plagiotropous stolons with elongated internodes show, however, orthotropous branches, and we, therefore, have on the same shrub branches which react differently to the light, some that are stoloniferous and plagiotropic, others that are leaf-bearing and orthotropic. After a time, however, the bushes assume a different habit by a suppression of parts, so that the older stems show two horizontally directed branches (plagiotropic), which separate from the common stem in a dichotomous manner. Now if we examine figs. 1 and 2 of Pl. XXV, we see that all of the lateral spurs that are formed from such a plagiotropic branch are placed on the upper side (orthotropous), where their leaves receive to the best advantage the light which filters down through the leafy canopy above. Each segment of such a branch represents a sympodium, where there are a series of phytons placed one after the other in serial order. By this method of sympodial branching, each new branch with the suppression of a bud on the other side and torsion of the axis, terminates in a leafy extremity, and the elongation of the branch according to this arrangement depends on a lateral bud (fig. 3). In this case clearly, as all of the leaves are directed dorsiventrally by light relationship, the permanent branching system is determined largely by the influence which the light has had in producing a one-sided growth of the lateral dichotomous branches of the adult plants. The fruit stands vertically above the broad, cordate leaves, as shown in figs. 4 and 5. Attention might be directed in closing to the color change which takes place in the leaves with the approach of autumn. The leaves become bronzed to a greater or less extent. Sometimes the bronze is in the form of blotches. In other leaves one side is bronzed, the other side is green, and in many examples the whole leaf rapidly bronzes. What induces the bronzing of one side of the leaf first, while the other side remains of a bright green color? Is it a light reaction? The photograph in Pl. XXIV was taken by Mrs. Harshberger; the drawings reproduced in Pl. XXV were made from rough drawings and data furnished Mr. Louis Schmidt by the writer.



HARSHBERGER ON INFLUENCE OF LIGHT.



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